THE REPLACEMENT OF ONE GRASSHOPPER SPECIES BY ANOTHER

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By Claude Wakeland,[1] *entomologist, Plant Pest Control Division, Agricultural Research Service*

The migratory grasshopper (*Melanoplus bilituratus* (Walk.)) [2] was numerically predominant in 1938 in nearly all counties of Montana, North Dakota, and South Dakota and in most counties of eastern Wyoming, western Nebraska, northeastern Colorado, and northwestern Kansas. It was then replaced in predominance in many areas by the differential grasshopper (*Melanoplus differentialis* (Thos.)). This replacement began to be obvious in 1939, when the differential grasshopper migrated northward by successive short-distance flights from its habitat along the White River in southwestern and the Missouri River in southeastern South Dakota until adults became conspicuous as far north as the vicinity of Pierre, S. Dak. During succeeding years the differential grasshopper continued to spread and increase in numbers until it became predominant as far northwest as Treasure and Rosebud Counties, Mont. It became predominant also outside of its habitat in most counties of South Dakota and in a few counties of western North Dakota, northwestern Nebraska, northwestern Kansas, and northeastern Colorado.

Grasshopper control to be successful should be based on a knowledge of the species and populations present in any area to be treated. Such knowledge is gained only by an on-the-ground survey. Although the predominant species can readily be determined by a survey, its relative predominance is ascertained only after sufficient data are accumulated so that comparisons can be made over several years.

A survey to determine grasshopper-control needs in many Western and Midwestern States was made from 1938 through 1955 by the Grasshopper Control Project, U.S. Department of Agriculture, with the cooperation of State and Federal research workers. The survey data analyzed in this publication covered parts of Montana, North Dakota, South Dakota, Wyoming, Nebraska, Colorado, and Kansas, where it was noticeable that the differential grasshopper was replacing the migratory grasshopper during this period. The survey was most thorough from 1938 to 1943. Thereafter it had to be curtailed because of a reduction in personnel. From the standpoint of analysis and comparison, a complete survey would have been desirable every year; however, from the standpoint of control, a survey generally was not necessary in many areas where populations were known to be low. The results of this study are not intended as a means of forecasting outbreaks or of displacing grasshopper surveys but of showing trends in population predominance that become apparent only after surveys are made in successive years.

Harmful infestations of the migratory grasshopper in crop areas may be both fieldwide and in field margins at the beginning of the season. Infestations of the differential grasshopper are mainly in the field margins immediately after the eggs hatch in the spring, but nymphs may migrate later into the fields. Control work, therefore, requires less material, machinery, and manpower for the differential species and consequently less financing and preparation. For instance, 81,240 tons (dry weight) of bait were used in Montana, North Dakota, and South Dakota in 1939 when the migratory grasshopper was the principal species to be controlled. However, when the differential grasshopper reached its peak in 1945, only 6,006 tons of bait were used in the same States. The differential grasshopper was much more numerous in many field margins in 1945 than the migratory grasshopper had been in any area in 1939. Therefore, baiting was mainly restricted to the margins in 1945, but it had been fieldwide over large areas of crop, range, and idle land in 1939. When baiting was directed against the migratory grasshopper, it was conducted in many more counties than when directed against the differential grasshopper.

[1] Retired August 1958.

[2] Until recently the name *Melanoplus mexicanus* (Sauss.) was widely used for this species. The taxonomy of *M. bilituratus* is discussed by A. B. Gurney and A. R. Brooks in U.S. Natl. Mus. Proc. 110, pp. 1–93 (1959). The common name, migratory grasshopper, remains unchanged for *bilituratus*.

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THE DIFFERENTIAL GRASSHOPPER IN MONTANA AND NORTH DAKOTA, 1932–38

To verify the presence of the differential grasshopper in eastern Montana prior to 1939, J. H. Pepper, of the Montana Agricultural Experiment Station, and J. R. Parker, formerly in charge of grasshopper research, U.S. Department of Agriculture, were consulted. Parker supplied information on the species in western North Dakota.

A résumé of their data shows that from 1932 through 1938 the differential grasshopper was reported from eastern Montana and western North Dakota as follows:

1932

Pepper collected the differential grasshopper in Dawson County, Mont., in 1932. That was the first record of its occurrence in Montana, and he assumed that it had been accidentally introduced there.

1933

Parker found a few specimens of the differential grasshopper in McLean and Mercer Counties, N. Dak., in 1933.

1934

Survey data of the Department for 1934 showed that in eastern Montana the differential grasshopper was second in predominance at one stop and present at two stops in Custer County, but it was not found in the six other counties surveyed.

In western North Dakota it was predominant at one stop in Golden Valley County, one stop in Adams County, and two stops in Morton County. In the same area it was second in predominance at one stop in Stark County, two in Hettinger County, and one in Sioux County. It was also present in Burke, Williams, Mountrail, McKenzie, Dunn, Mercer, Oliver, Slope, and Grant Counties.

In 1934 R. L. Shotwell [3] recorded that the two-striped grasshopper (*Melanoplus bivittatus* (Say)) and the differential grasshopper began building up in 1928 in North Dakota and reached their peak of abundance in the widespread outbreaks of 1931 and 1932. Although the weather was rather hot and dry during these years, food was abundant because of succulent crops. As the drought increased in 1933 and 1934 and the crops were ruined, these species almost disappeared.

1935

In western North Dakota in 1935 the differential grasshopper was predominant at one stop in Slope County, second in predominance at three stops in Adams County and two in Hettinger County, and present in Morton and Sioux Counties. Information for eastern Montana in 1935 is not available.

In 1935 Shotwell [4] reported that in the cropped area of Golden Valley and Stark Counties, N. Dak., the population of the differential grasshopper was increasing slightly.

1936

In eastern Montana this species was not found in the six counties surveyed in 1936. In western North Dakota it was second in predominance at one stop in Morton County, present in Stark County, but not found in the 12 other counties surveyed.

1937

In eastern Montana in 1937 this species was predominant at one stop and second in predominance at one stop in Custer County, but it was not found in the 14 other counties surveyed. In western North Dakota it was predominant at one stop and second in predominance at one stop in McLean County, but it was not found in the 10 other counties surveyed.

1938

Although the differential grasshopper was not mentioned in the 1938 report of the control survey and consequently is not shown in figure 3 of this report, Shotwell [5] stated that it was the predominant species in Richland County, Mont.

RECORDING SPECIES PREDOMINANCE, 1938–55

A study was made of 52,869 field notes of the 147 State and Federal men who conducted the grasshopper survey from 1938 through 1955 and of the weather records from 1931 through 1955 to determine the extent of species replacement and underlying causes. Many species were recorded, including the predominant species, those second in predominance, and other unusually abundant species.

For each county surveyed, the percentages of predominance were determined for the migratory

[3] *In* Parker, J. R. FOURTH QUARTERLY REPORT, p. 6. 1934. [Unpublished.]

[4] *In* Parker, J. R. THIRD QUARTERLY REPORT, p. 6. 1937. [Unpublished.]

[5] Shotwell, R. L. THE SPECIES AND DISTRIBUTION OF GRASSHOPPERS IN THE 1937 OUTBREAK. U.S. Bur. Ent. and Plant Quar. Insect Pest Survey Bul. 18 (6, sup.): 385–443. 1938.

and the differential grasshoppers in relation to all grasshopper species recorded at each stop. The average percentages of predominance and of second in predominance for these two species for each county surveyed were recorded on maps depicting States and counties. A high percentage of predominance for one species might not mean it was economically important, for the population of all grasshopper species might have been low during certain years.[6] A map showing the percentages of predominance for the migratory grasshopper for each county surveyed in 1938 is given in figure 1.

The areas of predominant species and of species second in predominance were then outlined on these maps, and the outlines were traced on maps showing only State boundaries. The patterns of predominance for the migratory and the differential grasshoppers were then drawn on these maps for each of the 18 years studied, as shown in figures 2 and 3, respectively.

REPLACEMENT OF SPECIES

Many species were present in the crop areas of the region studied. In addition to the migratory and the differential grasshoppers, the principal species were the two-striped grasshopper, the red-legged grasshopper (*Melanoplus femur-rubrum* (DeG.)), *Aeoloplides turnbulli bruneri* (Caud.), the clear-winged grasshopper (*Camnula pellucida* (Scudd.)), and the Packard grasshopper (*Melanoplus packardii* Scudd.). This study was restricted to the migratory and the differential grasshoppers, because it was obvious in the control operations that replacement of these species was taking place annually. A similar replacement of other species could probably have been shown if more comprehensive studies had been made.

Although control measures were primarily directed against the migratory grasshopper from 1938 through 1940, the differential grasshopper frequently was second in predominance in many counties. In some counties the migratory grasshopper was predominant at control time, but the differential grasshopper was predominant in the fall survey.

When the differential grasshopper began replacing the migratory species, it nearly always was second in predominance for a year or more before it became predominant (fig. 3). This replacement continued until 1945. By 1950 the differential grasshopper was not predominant in any county of Montana or North Dakota and of little economic importance elsewhere in the region studied. It continued to be of little economic importance, except in localized areas for the rest of this study.

Although the migratory grasshopper was replaced by the differential grasshopper, the latter species, when it receded, was first replaced by other species indigenous to the different localities. In Montana, North Dakota, western and northern South Dakota, and western Nebraska, the chief replacement was the two-striped grasshopper; in the eastern Dakotas and in eastern Nebraska, the red-legged grasshopper; and in western Kansas and eastern Colorado, *Aeoloplides turnbulli bruneri*. This replacement in a locality was not always by a single species. For example, in South Dakota the replacement was mainly by the two-striped grasshopper in the west and by the red-legged grasshopper in the east. Various proportions of the two species were present in the counties between these sections.

During these studies the migratory and differential grasshoppers were recorded in many counties throughout the region, but they were not the predominant species except as shown in figures 2 and 3, respectively. Apparently the order of transition back to predominance of the migratory grasshopper, as affected by prevailing natural conditions, is after the predominance of other indigenous species.

The average percentage of predominance of a species, which changed from year to year, is not reflected in figures 2 and 3, as illustrated by the following examples: The black areas denoting predominance of the migratory grasshopper in Montana and North Dakota in 1938 and 1939 are identical, but its predominance there averaged 96 percent in 1938 and only 87 percent in 1939. The predominant species in 17 counties in Montana in 1938 and 1940 was also the migratory grasshopper, but with averages of 99 percent in 1938 and only 80 percent in 1940. This species was second in predominance in North Dakota in 1950 and 1951; its predominance averaged 75 and 64 percent, respectively. It was second in predominance in the same 10 counties in North Dakota in 1939 and in 1949, with averages of 26 percent in 1939 and 67 percent in 1949. It was also second in predominance in 18 counties in South Dakota in 1939 and 1948; the averages were 37 and 61 percent, respectively.

Figure 3 shows that the differential grasshopper invaded farther northward and westward from 1938 through 1945. Thereafter it generally receded. However, it was predominant in a few small areas but not economically important. It was not predominant in Montana and North Dakota after 1949, except in small areas, until 1951

[6] Unpublished data.

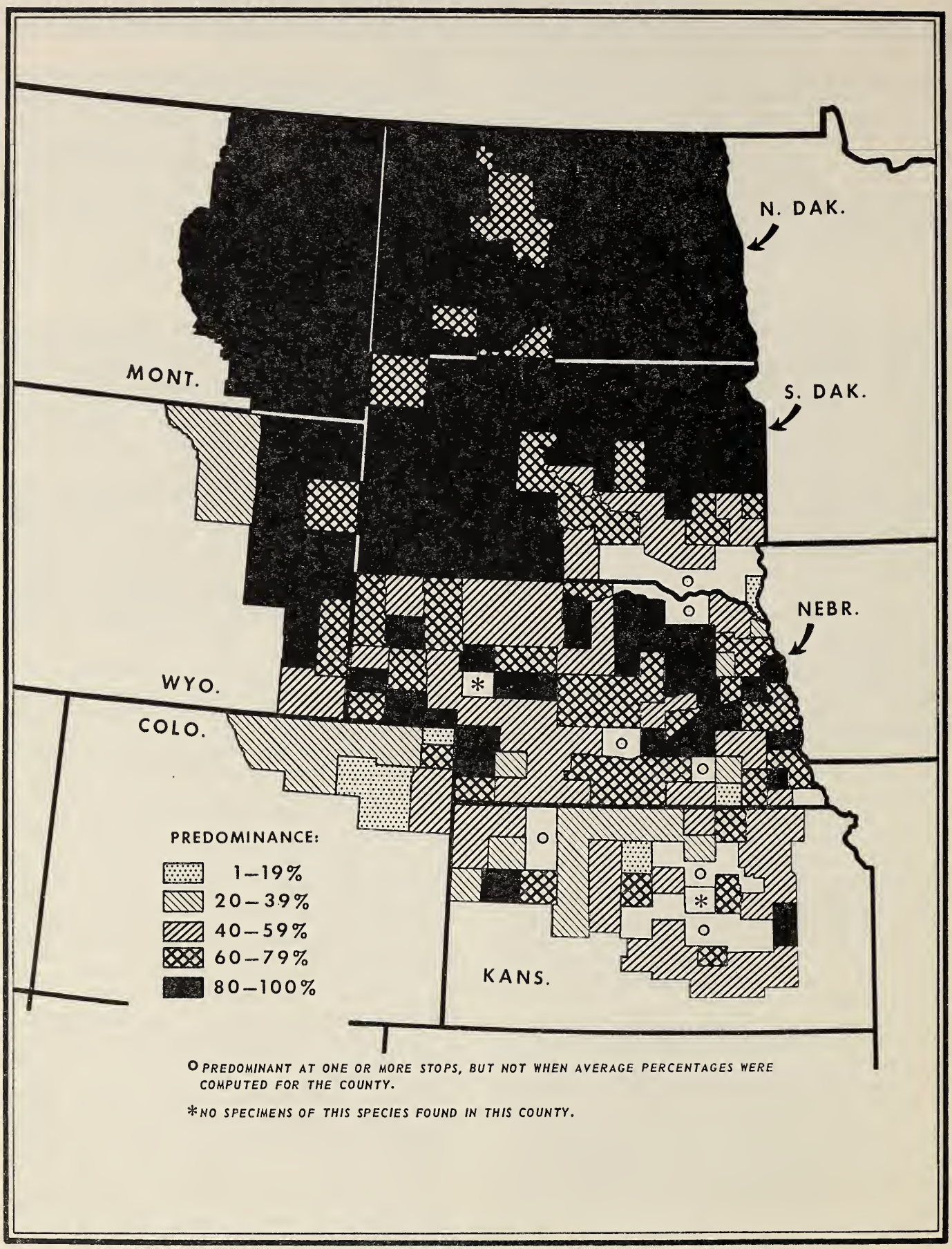

FIGURE 1.—Percentages of predominance by counties for the migratory grasshopper in 1938.

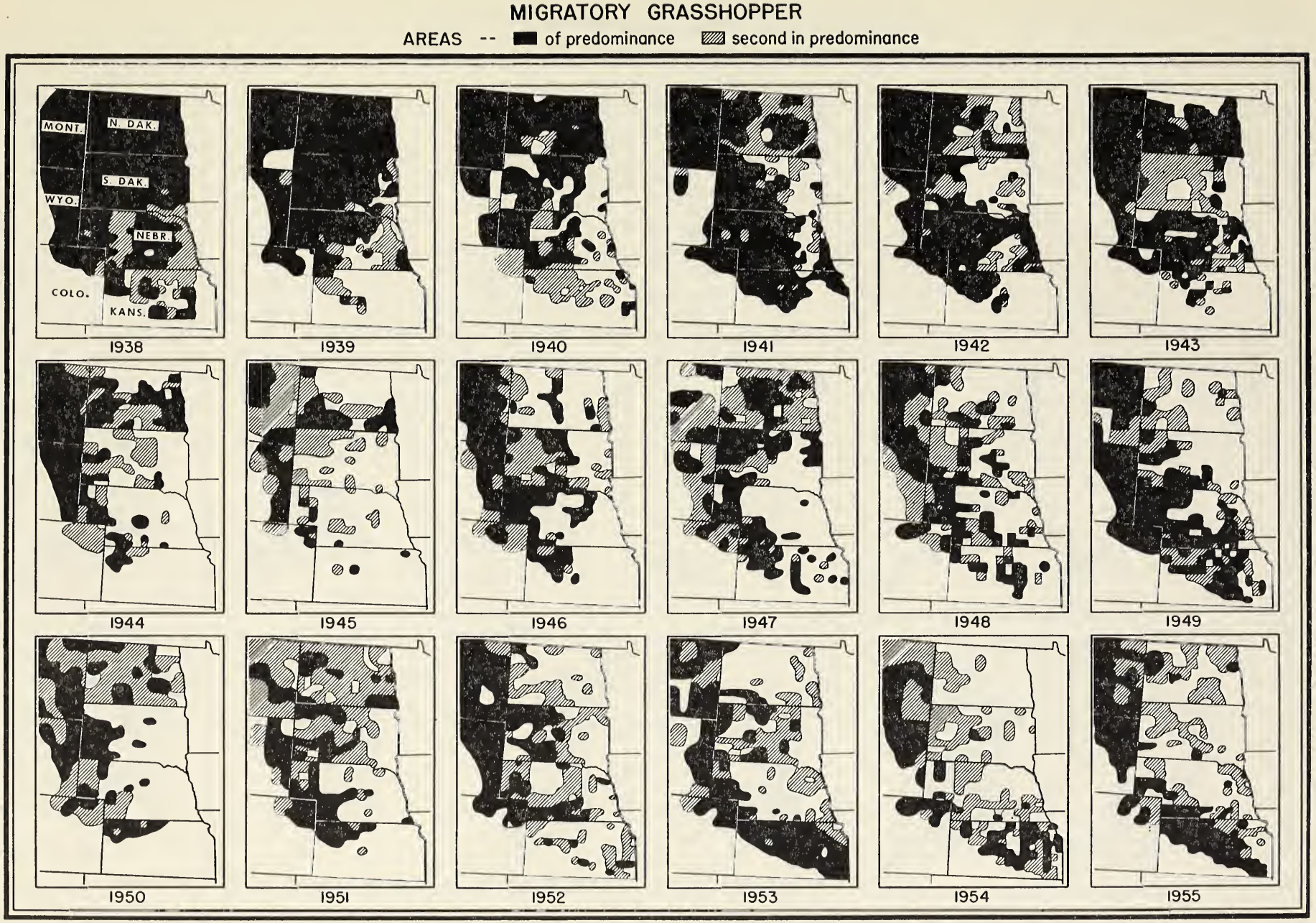

FIGURE 2.—Patterns of predominance for the migratory grasshopper in 1938–55.

FIGURE 3.—Patterns of predominance for the differential grasshopper in 1938–55.

and 1955. In 1951 it was predominant in the irrigated area along the lower Yellowstone River in Prairie and Richland Counties, Mont., and in one area in Adams County, N. Dak. However, it was not economically important in any of these counties. In 1955 it was predominant in McCone County, Mont., and in Sargent County, N. Dak., where it was of little economic importance.

The differential grasshopper is consistently of major economic importance in eastern Nebraska, but it was of little consequence in control operations from 1950 through 1955, when the average precipitation was about normal. It was predominant and second in predominance after 1949 in western and central Nebraska only in small areas along watercourses or in irrigated sections.

The differential grasshopper is usually predominant in eastern Kansas. Its spread into western Kansas in 1938 and 1939 was temporary. When populations persisted in later years, they were again chiefly in irrigated areas or in lands along watercourses. In 1955 there were striking build-ups of populations in eastern Kansas.

The migratory grasshopper was predominant and secondary in predominance in many counties throughout South Dakota during the entire study, but after 1948 the populations were small and the species was of little economic importance.

EFFECT OF WEATHER ON SPECIES REPLACEMENT

In a study of fluctuations in grasshopper populations many factors must be considered, such as weather, ecology, natural enemies, and reproductive capacity. The interrelation of such factors is complex and may never be fully understood nor the net result be measurable.

Weather appears to have been an important factor in the replacement in predominance of the migratory grasshopper by the differential grasshopper over extensive areas and in the spread of the latter species to areas where it previously had been of little or no economic importance. A study of voluminous survey data for guiding control operations throws some light on the effect that weather might have.

The differential grasshopper did not remain dominant for long in the areas invaded, for it receded to its habitat. Populations of the migratory grasshopper ordinarily decrease much less rapidly, because they are less susceptible to fungus or bacterial diseases than populations of the differential grasshopper. These diseases often become epidemic with the differential grasshopper when precipitation is greater than usual during warm weather.

Grasshopper control is more difficult and is required more frequently when the annual precipitation is low, especially where the migratory grasshopper is predominant. The region studied lies within two precipitation zones—one with 20 inches or less and one with more than 20 inches annually.

U.S. Weather Bureau records were studied from 1931 through 1955 for the following stations in the zone of 20 inches or less:

Fort Collins, Colo.	Jamestown, N. Dak.
Goodland, Kans.	Hettinger, N. Dak.
Scottsbluff, Nebr.	Mandan, N. Dak.
Wheatland, Wyo.	Williston, N. Dak.
Belle Fourche, S. Dak.	Billings, Mont.
Mobridge, S. Dak.	Glendive, Mont.
Pierre, S. Dak.	Malta, Mont.

In localized areas where sufficient eggs are present to produce a large population of nymphs, the expected population does not always materialize. The chief cause is a protracted spell of wet, cool, or severely cold weather when the delicate nymphs emerging from the eggs are either killed or die of starvation because they are too chilled to feed. Population reduction sometimes results from egg predatism, but this is usually anticipated when predators are present at the time of the egg survey the previous fall.

The migratory grasshopper increases in numbers and intensity of attack when the precipitation is low. The effect of total annual precipitation on population change did not fit the population patterns shown in figures 2 and 3, for increased or decreased populations were not evident after or during any 1 year of precipitation that was appreciably above or below normal. For example, in 1938 when the migratory grasshopper was more predominant than in any year studied, the precipitation was above normal, and in the preceding year it was normal, as shown in figure 4.

The population apparently was affected more by the weather in the years preceding than in the year when the survey was made or in the following year of control operations.

Precipitation as it affects grasshoppers may not be the most important weather factor, but it was studied because precipitation data were available and because outbreaks of the migratory grasshopper occur during prolonged periods of abnormally dry weather. A change in species is gradual and becomes readily recognizable only after several years of abnormal weather in the area as a whole. Precipitation records above or below normal for individual localities may be counterbalanced by records in other nearby localities, but the precipitation over a large area is likely to average above or below normal during critical periods in grasshopper development.

The greatest effect of weather on grasshopper development occurs during the period from hatching through the nymphal stage and into the early adult stage, when the abundance, palatability, and

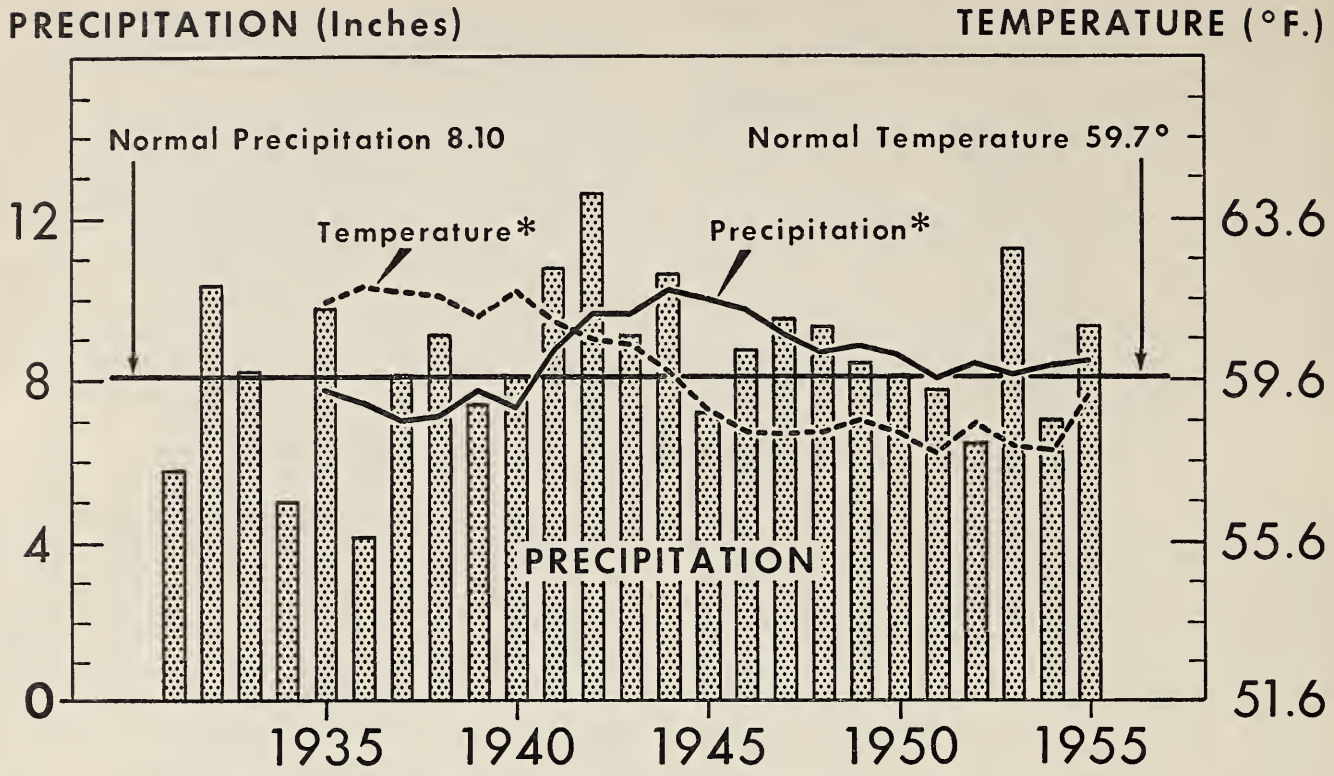

FIGURE 4.—Average precipitation and temperature from April through July in 1931–55.

nutrition of the food consumed determine the development of eggs for the next generation. This period is from April through July. Since normally the eggs of both species are deposited in the soil during 1 or 2 months in the fall and remain there for about 6 or 7 months, they are little affected by weather. Their abundance and viability already have been affected by the amount and type of food.

The effect of precipitation from April through July of single months and of combinations of 2, 3, and 4 months on populations was studied to determine whether the weather pattern was similar to the population pattern. The weather pattern most nearly fitting the population pattern in figures 2 and 3 occurred when the period from April through July was used and a 5-year average precipitation was calculated. So little difference was indicated as to whether the period was April–July, April–August, or May–August that the first period was used. Change of species took place over an extensive area. Therefore, 5-year averages were calculated for April through July for stations that were representative of the area.

A weather pattern became evident when the annual precipitation was considered as a 5-year average; that is, when the precipitation of any 1 year was added to that of the preceding 4 years and an average was taken. However, the weather pattern did not fit the population pattern very well (figs. 2–4).

The weather pattern was indefinite when the annual precipitation was considered as the factor that might have affected predominant populations of either species (fig. 4). Although it is evident that from 1931 through 1935 there was more precipitation below than above normal, yet the precipitation for 3 of the 5 years was above normal. In 1935, when the 5-year average precipitation was calculated, the precipitation for April through July was 96 percent of normal; in 1936, 92 percent; in 1937, 80 percent; in 1938, 82 percent; and in 1939, 94 percent.

The 5-year average precipitation continued to rise until 1944, when it reached 125 percent of normal. The severe infestations of the migratory grasshopper in 1938 and 1939 followed 7 years when this average was less than normal from April through July. The spread of predominant populations of the differential grasshopper became conspicuously noticeable in 1941, when the 5-year average precipitation was above normal, and continued until 1949, when it was above normal for 9 consecutive years. This species reached its peak of predominance and of area infested in 1945. Thereafter, the 5-year average precipitation began to decrease, but residues of predominant populations remained until 1951, when the average

fell below normal for the first time in 10 years.

The migratory grasshopper was predominant when the 5-year average precipitation was appreciably below normal. The differential grasshopper was predominant, invaded new territory, and replaced the migratory grasshopper when the 5-year average precipitation was above normal.

No attempt was made to correlate temperature with precipitation, although the 5-year average temperature is plotted in figure 4. Obviously the 5-year average temperature was high when the precipitation was low. Probably a high temperature during drought periods was favorable to the rapid development of the migratory grasshopper, but the drought was unfavorable to the growth of succulent vegetation on which the differential grasshopper thrives. Conversely, a low temperature with above-normal precipitation was unfavorable to the migratory grasshopper but favorable to the differential grasshopper.

Temperature affects the populations of grasshopper species and the abundance and palatability of plants upon which they feed, but to what extent can only be assumed from these studies. Precipitation deviations were, of course, much greater than temperature deviations. The average precipitation for all stations for the April-July period ranged from 82 percent below to 125 percent above normal. The average temperature ranged only from 10 percent below to 12 percent above normal.

CONCLUSIONS

Populations of the migratory grasshopper increased and spread when the 5-year average precipitation for April through July was below normal, whereas populations of the differential grasshopper increased and spread when this average was above normal. When the precipitation was considerably above normal, the migratory grasshopper was replaced in predominance by the differential grasshopper, and the latter species became predominant in areas much farther north and west than it had been previously. When the 5-year average precipitation approached normal again, the differential grasshopper receded to its habitat and populations generally became of minor economic importance. This species was not replaced by the migratory grasshopper at first but by other species indigenous to the particular area.

U.S. GOVERNMENT PRINTING OFFICE: 1960